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Microsite Occupancy and the Spatial Structure of Understorey Regeneration in Three Late-Successional Norway Spruce Forests in Northern Europe

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We compared microsite occupancy and three spatial structure of regeneration in three primeval late-successional Norway spruce dominated forests. One area lay in the middle boreal zone in Russia (Dvina-Pinega) where larger-scale disturbance from bark beetles and drought had occurred; the other areas lay in the northern boreal zone, one in Finland (Pallas-Ylläs) had encountered only small-scale disturbance, and one in Russia (Kazkim) had been influenced by fire. We mapped all spruce (*Picea abies*) and birch (*Betula pendula* and *Betula pubescens*) trees with diameter at breast height (DBH) ≥ 10 cm on 40 m × 400 m plots, and those with DBH < 10 cm on 2 m or 4 m × 400 m subplots. On the subplots we also recorded microsite occupancy and estimated microsite availability. At all study areas small seedlings (h < 0.3 m) of both spruce and birch were found largely on disturbance-related microsites. Birch saplings (h ≥ 1.3 m, DBH < 10 cm) disproportionately occupied deadwood-related microsites at Dvina-Pinega. In contrast, spruce saplings at all study areas, and birch saplings at Kazkim and Pallas-Ylläs, showed less, or no, preference. Our results thus confirm the importance of disturbance-related microsites for regeneration establishment, but not necessarily for long-term survival. No spatial segregation between the overstorey (DBH ≥ 10 cm) and saplings (h ≥ 1.3 m, DBH < 10 cm) or seedlings (h < 1.3 m) was found at Pallas-Ylläs or Kazkim, and only three instances of very weak segregation were found at Dvina-Pinega. This suggests that the regeneration gap concept may not be useful for describing the regeneration dynamics of primeval boreal forests.

Keywords disturbance, boreal forests, natural forests, spatial correlation, stand structure
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1 Introduction

In boreal forests localised autogenic disturbances are important for regeneration where climatic and edaphic conditions make the ignition and spread of fire improbable (Sernander 1935, Wallenius et al. 2005, Fraver et al. 2008). The Norway spruce (*Picea abies* (L.) Karst.) forests of boreal northern Europe fall into this category. Chronic local perturbations evoke resource heterogeneity through overstorey tree mortality and substrate changes (Lundqvist and Fridman 1996, Gray and Spies 1997, Franklin and Van Pelt 2004).

Substrate disturbance is particularly important in Norway spruce dominated forests due to the ubiquitous moss-humus mat which physically impedes regeneration and diminishes resource availability (Sirén 1955). Disturbance can expose the mineral soil and alter the abundance and diversity of regeneration microsites (Harper 1977, Harmon and Franklin 1989). Disturbance microsites may constitute 'safe sites' (*sensu* Harper 1977) for regeneration, primarily due to reduced competition from herbs and mosses (Harmon and Franklin 1989) and favourable moisture supplies (Place 1955).

Microsite type may influence species composition (Hörnberg et al. 1997, Kuuluvainen and Juntunen 1998); coniferous species have been found to preferentially occupy deadwood (Hofgaard 1993, Lilja et al. 2006), while deciduous species show some preference for uprootings (Vodde et al. 2011). However, it has been suggested that disturbed microsites may be less advantageous for long-term survival (Kathke and Bruelheide 2010). For example, intense competition can arise on deadwood between seedlings (Kuuluvainen and Kalmari 2003, Vodde et al. 2010) and from other vascular plants (Harmon and Franklin 1989, Zielonka 2006), while uprootings may be highly unstable (Vodde et al. 2011).

Overstorey tree mortality in high latitude boreal forests does not create 'canopy gaps' comparable to those in temperate forests (Kuuluvainen 1994, McCarthy 2001, Bartemucci et al. 2002). This is primarily due to the overall sparse canopy cover and low sun angles which prevent significant changes in the availability of light in gaps (Pukkala et al. 1991, Kuuluvainen 1994, Ban et al. 1998). Below ground impacts of allelopathy and resource competition may also be more important than changes in light conditions (Kuuluvainen 1994, Zackrisson and Nilsson 1992).

Repeated local disturbance and infilling is understood to lead to fine-scale variability within a relatively homogenous matrix (McCarthy 2001) which may endure in shifting steady-state mosaic for centuries (Bormann and Likens 1979, Aakala et al. 2009, Shorohova et al. 2009). However, moderately severe disturbance (Aakala et al. 2009, Fraver et al. 2008) can initiate patch dynamics (McCarthy 2001), typified by a coarse-grained landscape of patches in various seral stages (Oliver and Larson 1996). Norway spruce advance regeneration can persist for centuries, often on deadwood, before acclimating to increased resources due to canopy tree mortality (Leemans 1991, Qinghong and Hytteborn 1991). Localised disturbed gaps therefore tend to perpetuate spruce domination (Leemans 1991, Hofgaard 1993). More severe disturbance can remove the spruce advance regeneration and provide advantageous mineral soil substrate and light conditions which benefit light-demanding deciduous species (Ilisson et al. 2005, Vodde et al. 2010, Vodde et al. 2011). Climatic influence may accentuate the severity of disturbance and increase background mortality (Hofgaard 1993, Hörnberg et al. 1995, Aakala and Kuuluvainen 2011). However, gaps and patches are human inventions and functional heterogeneity may not correspond to observed heterogeneity (Bazzaz and Wayne 1994).

The subject of this study is regeneration in old Norway spruce forests. The aim was to characterise and compare two aspects of the regeneration processes – namely the spatial structure of regeneration and microsite occupancy – in three areas of primeval (having negligible direct human impact) Norway spruce-dominated forest. We characterised the regeneration processes at each study area by asking:

1) Are disturbed microsites preferentially occupied?
2) Does microsite preference vary between different regeneration strata?
3) Does regeneration exhibit spatial correlation?
4) Are the regeneration strata spatially segregated from the overstorey stratum?

We also briefly describe density, volume and species composition. Preferential occupation of disturbed microsites may indicate that substrate is an important determinant of regeneration. Differences in microsite preference between regeneration strata may suggest the substrates which facilitate establishment and early growth differ to those beneficial for recruitment success. Local spatial correlation of the regeneration strata could signal a fine-scale spatial mosaic driven by local disturbance. We may expect local spatial segregation of these strata if the spatial pattern of regeneration is largely ordained by above-ground overstorey changes (Larson and Franklin 2006).

The study areas are located in distinct geographic locations with contrasting disturbance histories known from previous studies (Aakala et al. 2009, Caron et al. 2009, Aakala et al. 2011) and have developed for an extended time without the occurrence of stand-replacing disturbance.

2 Material and Methods

2.1 Study Areas

The studies were conducted in three different unmanaged spruce dominated forest areas in the boreal zone of northern Europe (Fig. 1). The areas differed in their vegetation zone classification (Ahti et al. 1968). Two areas were in the northern boreal zone: the Pallas-Ylläs National Park in north-western Finland (67°40’N, 24°22’E) and the Kazkim river area of the Laplandsky Forest conservation area situated in the Murmansk Province of the Russian Federation (68°18’N, 30°22’E). The third study area was located in the forest massif between the Dvina and Pinega rivers in the middle boreal vegetation zone in Arkhangelsk Province, Russian Federation (63°00’N, 44°10’E). In the study forests shade-tolerant, long-lived Norway spruce (*Picea abies* (L.) Karst.) occurred with an admixture of shade-intolerant birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) and occasional pines (*Pinus sylvestris* L.). The field-layer was dominated by mosses (mainly *Hyloconium splendens* and *Pleurozium schreberi*), and shrubs such as *Vaccinium myrtillus*, *Vaccinium vitis-idea*, *Vaccinium uliginosum*, *Juniperus communis*, *Empetrum nigrum* and *Ledum palustre*.

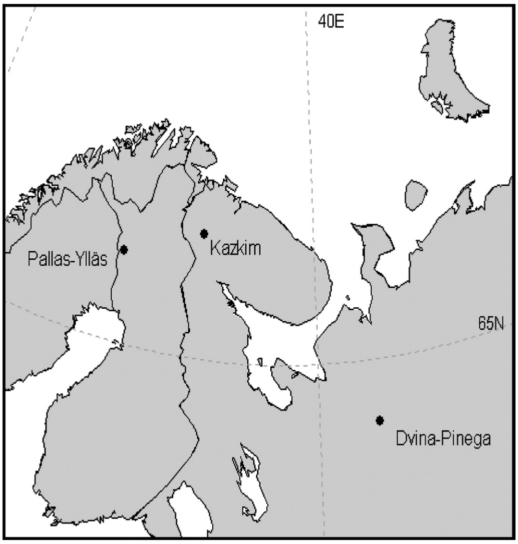

Fig. 1. Study area locations.

The study forests lie approximately between 200 and 400 m above sea level (a.s.l.) at Pallas-Ylläs, whilst the elevation ranged from approximately 100–200 m a.s.l. at Kazkim and Dvina-Pinega. The annual precipitation exceeds evapotranspiration at all study areas, and is 500 mm at Pallas-Ylläs of which 41% is solid, 550 mm at Kazkim of which 35% is solid, and 670 mm at Dvina-Pinega of which 37% is solid. The mean temperatures of the warmest and coldest months respectively are 14.1˚C (July) / –15.2˚C (January) at Pallas-Ylläs, 13.0˚C (July) / –14.7˚C (February) at Kazkim, and 17.2˚C (July) / –13.2˚C (January) at Dvina-Pinega (precipitation and temperature both from the FAO CLIM 2.0 database, United Nations Food and Agriculture Organization).

2.2 Study Area Disturbance History

Contrasting past disturbance regimes have been documented in the study areas (Aakala et al. 2009, Aakala et al. 2011). At Dvina-Pinega, episodic tree mortality defines the past disturbance regime. These episodes are thought to be due to the combined effects of drought and the spruce bark beetle (*Ips typographus* L.) (Aakala et al.

2011, Aakala and Kuuluvainen 2011). In a recent bark beetle and drought event between 1999 and 2004, approximately 21% of trees were killed in the study area (Aakala et al. 2011). The disturbance regime at Dvina-Pinega is therefore a background of constant small-scale events punctuated by infrequent events of moderate severity (Aakala et al. 2011).

In contrast, the majority of the trees at Kazkim represent a distinct relatively even-aged cohort which has arisen following a stand-replacing fire that occurred 1689 (Aakala et al. 2009). Synchronous natural senescence has had a pronounced influence on the dynamics. The mortality rates of 0.9% and 0.3% respectively for Kazkim and Pallas-Ylläs demonstrate the difference between the two areas (Aakala et al. 2009).

The forest at Pallas-Ylläs has escaped allogenic disturbance for a period of at least 400 years, but possibly up to 1000 years (Caron et al. 2009). Pallas-Ylläs has a lesser proportion of elderly trees, and the disturbance dynamics are apparently dominated by the deaths of single trees or small groups of trees (Caron et al. 2009).

The study plots at all study areas were used in previous studies on tree mortality and deadwood dynamics (Aakala et al. 2009, Aakala et al. 2011, Aakala and Kuuluvainen 2011). The plots were selected as being representative of unmanaged, late-successional spruce dominated forest. During the selection process a visual analysis was also made to ensure that the plots were edaphically homogenous to each other.

2.3 Methods

Five 40 m × 400 m plots were used at all study areas, and within them all living and dead trees (including fallen dead trees, these components are henceforth referred to as overstorey and deadwood respectively) with a breast height diameter of at least 10 cm were mapped, and species and DBH recorded. In all the study plots, tree height measurements were made on a subsample comprising approximately half of the total number of trees. The heights of the remaining trees were estimated using regression models between DBH and tree height (Aakala et al. 2009). Decay class was assigned following the system in Aakala et al. (2009). Wood volumes were calculated using volume integrals of taper equations devised by Laasasenaho (1982).

Within each plot a smaller subplot was used for studying regeneration. The subplot was delineated symmetrically around the plot midsection. At Kazkim and Pallas-Ylläs the subplot size was 4 m × 400 m. At Dvina-Pinega the subplot size was 2 m × 400 m, due to the higher regeneration density. Within the subplots all trees with a minimum height of 0.1 m and a DBH < 10 cm were mapped with a longitudinal coordinate only. Birch stool sprouts were included in the counts. Height was measured for all trees with a height (h) < 1.3 m, and for the majority of the trees taller than that, although not all trees were measured due to time restrictions. Regression models were used to model the heights for the remaining trees with a DBH ≥ 1 cm (39% of trees at Kazkim and less than 0.5% at Dvina-Pinega and Pallas-Ylläs).

The type of microsite on which the individual was found growing was recorded. Microsite type was also recorded at 1 metre intervals along the longitudinal midsection of the plot, thus providing a systematic inventory of available microsites within the plot. A simple four-class system was employed where microsites were assigned to one of the following categories: 1) uprooting related (a root-plate mound or uprooting pit), 2) deadwood related (on or immediately beside deadwood (approx. ≤ 1 cm) in an advanced state of decay, covered by ground vegetation), 3) undisturbed (disturbance not evident) or 4) other. The disturbed microsite classification categories are deliberately broad to allow for ageing which could obscure the nature of the substrate where establishment actually occurred. For example, it may be impossible to establish the boundary between the pit and the mound of eroded uprootings. Similarly, if regeneration is found immediately beside a very decayed log, it is quite possible that initial establishment occurred on the deadwood substrate which has subsequently disappeared. Accordingly, in such cases the deadwood related classification was used only where the state of decay of the log was such that regeneration may have been associated with it. The time taken for a log to reach such an advanced state of decay varied between the study areas and was 40 years at Kazkim, 30 years at Pallas-Ylläs and 20 years at Dvina-Pinega (Aakala 2010). The undisturbed category represents the typical background forest floor matrix where physical disturbance was not evident and there was not a significant immediate discontinuity in elevation. The 'other' category comprises relatively rare, atypical discontinuities which do not belong in the three primary categories, for example rocky outcrops, anthills and ponds.

2.4 Statistical Analysis

The significance of microsite occupation was tested using a G-test for goodness-of-fit (Sokal and Rohlf 1995). The G-test for goodness-of-fit (Eq. 1) detects if the regeneration microsite occupancy significantly deviated from the surveyed proportions of the four microsite categories at each area. The null hypothesis is that microsite occupancy is not significantly different from availability. Separate tests were performed for three height strata: (1) small seedlings ($h < 0.3$ m), (2) seedlings ($h > 0.3$ m, < 1.3 m) and (3) saplings ($h \geq 1.3$ m, $DBH < 10$ cm). Birch sprouts were removed from the analysis as they are asexual. Data for all five transects were pooled as the intention was to explore variability between the study areas.

The G-test is formally defined as follows:

$$G = 2\sum_{i=1}^{k} o_i \ln \frac{o_i}{e_i} \qquad (1)$$

where G is the test statistic and o_i and e_i are the observed frequency (occupation frequency) and availability frequency for microsite class i (from k possibilities) respectively.

Spatial correlation and cross-correlation functions were estimated with spline correlograms. We estimated spatial cross-correlation between the overstorey stratum ($DBH \geq 10$ cm) and saplings ($h \geq 1.3$ m, $DBH < 10$ cm) or seedlings ($h < 1.3$ m). The spatial correlation of saplings and seedlings were also estimated separately. We used the *R* library 'ncf' ($df = 7$; *R* package version 1.1-3, Bjørnstad 2005). 95% upper and lower confidence envelopes were constructed using a bootstrapping algorithm based on 1000 bootstrap instances (Bjørnstad and Falck 2001). Seperate spline correlograms were made for each subplot to allow within-area variability to be examined.

Spline correlograms have two values of ecological significance (Seabloom et al. 2005). The first is the value of the spatial correlation at a lag distance of 0 (*y*-intercept). This value denotes the strength of local spatial attraction (positive values) or segregation (negative values). Local spatial correlation is therefore not significant where the 95% confidence envelope spans the *x*-axis at the *y*-intercept point. The value of the *x*-intercept shows the spatial upper limit to the clumping or dispersion. This method facilitates detection of spatial correlation of variables which is not possible with other bivariate statistical methods.

To facilitate these analyses the plots were subdivided into 49 overlapping circular cells. The cells had a diameter of 16 m, and the first one was centred at 8 m and the last at 392 m on the *x*-axis. Each cell overlapped by 8 m with the preceding cell to model a window of influence on the regeneration occurring within each cell. The weighted basal area (BA) of living overstorey trees was totalled for each overstorey cell by dividing the BA of each tree by its distance from the cell midpoint and summing the weighted values. The number of seedlings ($h < 1.3$ m) and saplings ($h \geq 1.3$ m, $DBH < 10$ cm) within each regeneration cell (only *x*-coordinates were recorded for regeneration) were separately counted.

It is recognised that the scale of observation can affect both the strength and spatial extent of spatial relationships (Larson and Franklin 2006). Spatial structures are universally subject to such scale-dependency, and the present study therefore gives information about the structure detected at one scale which was consistent for all the study areas.

3 Results

3.1 Forest Characteristics

The densities of living overstorey trees ($DBH \geq 10$ cm) were higher at Dvina-Pinega than at Pallas-Ylläs and Kazkim which were more similar to each other (Table 1). The volume of over-

Table 1. Living tree volumes and densities (includes asexual regeneration).

Component	Dvina-Pinega	Pallas-Ylläs	Kazkim
Density (number/ha)			
Living overstorey trees	502 (76)	458 (59)	452 (39)
Regeneration			
Seedlings	5635 (2754)	1239 (326)	1303 (469)
Saplings	1023 (200)	418 (186)	1555 (244)
Volume (m^3/ha)			
Living overstorey trees	150 (21)	106 (17)	66 (7)

(values in parentheses are standard deviation)

Table 2. Species composition of forest components, expressed as percentage share (includes asexual regeneration).

Component	Dvina-Pinega			Pallas-Ylläs			Kazkim		
	Spruce[1]	Birch[2]	Pine[3]	Spruce	Birch	Pine	Spruce	Birch	Pine
Density (number/ha)									
Living overstorey trees	92.0	7.9	0.1	66.0	32.3	1.7	62.3	36.6	1.1
	(9.6)	(9.7)	(0.1)	(8.2)	(7.0)	(2.1)	(8.4)	(8.1)	(0.7)
Regeneration									
Seedlings	90.7	9.3	0.1	65.4	33.6	1.0	14.4	85.5	0.1
	(3.6)	(3.6)	(0.1)	(9.9)	(9.2)	(1.2)	(11.4)	(11.3)	(0.2)
Saplings	85.2	14.8	–	63.7	35.3	1.1	12.6	87.4	–
	(10.1)	(10.1)	–	(14.9)	(13.7)	(1.8)	(6.6)	(6.6)	–
Volume (m^3/ha)									
Living overstorey trees	87.6	12.0	0.2	77.6	17.4	5.4	77.0	19.6	3.6
	(12.2)	(12.5)	(0.4)	(9.9)	(5.9)	(5.8)	(7.0)	(5.9)	(2.6)

(values in parentheses are standard deviation, values may not total 100% due to rounding)
[1] *Picea abies*; [2] *Betula pubescens / Betula pendula*; [3] *Pinus sylvestris*

storey trees at Dvina-Pinega was also higher than that of the other two study areas at 150 m^3 ha^{-1} but in contrast to the density the overstorey volume of 66 m^3 ha^{-1} at Kazkim was much lower than at Pallas-Ylläs 106 m^3 ha^{-1}. The density of seedlings ($h < 1.3$ m) and saplings ($h \geq 1.3$ m, $DBH < 10$ cm) was elevated at Dvina-Pinega, at 5635 and 1023 per ha respectively. The other two study areas had more similar seedling densities at 1239 per ha at Pallas-Ylläs and 1303 per ha at Kazkim. At Kazkim the density of saplings was 1.2 times greater than the seedling density. At Pallas-Ylläs saplings were only 0.3 times as dense as seedlings, and 0.2 times as dense at Dvina-Pinega.

The species composition of both the overstorey and regeneration at Dvina-Pinega and Pallas-Ylläs was dominated by spruce (Table 2). The species composition of regeneration at Kazkim was dominated by birch, while Dvina-Pinega had the lowest proportions of birch in all components. There was no asexual birch regeneration (sprouting) at Dvina-Pinega. At Pallas-Ylläs 11.3% (SD 11.9) of regeneration was sexual (from seed) and 88.7% (SD 11.4) asexual, whereas at Kazkim 48.8% (SD 38.8) was sexual and 51.2% (SD 30.8) asexual.

3.2 Microsite Availability and Occupancy

The observed frequencies of microsite availability showed undisturbed ground to be the most abundant category at all study areas (Fig. 2). Of the available microsites, 40%, 68% and 74% were undisturbed at Dvina-Pinega, Pallas-Ylläs and Kazkim respectively. Approximately 60% of microsites at Dvina-Pinega were disturbance related, with an even split (30% each) between deadwood and uprooting related microsites. At Pallas-Ylläs some 15% of microsites were deadwood related and 10% uprooting related, while at Kazkim the frequencies were approximately 14%

Table 3. G-statistic for the deviation of microsite occupancy from availability. A significant p-value means that the microsite occupancy frequencies significantly deviate from the availability frequencies.

Variable	Dvina-Pinega		Pallas-Ylläs		Kazkim	
	Spruce[1]	Birch[2]	Spruce	Birch	Spruce	Birch
Small seedlings	113.7 *** n=1064	73.5 *** n=95	48.6 *** n=302	142.6 *** n=14	152.3 *** n=32	312.6 *** n=157
Seedlings	62.4 *** n=982	60.6 *** n=112	48.1 *** n=327	188.8 *** n=9	78.2 *** n=100	33.2 *** n=263
Saplings	4.99 n.s. n=343	64.84 *** n=66	4.8 n.s. n=200	26.4 *** n=11	1.43 n.s. n=157	1.53 n.s. n=465

(* $p < 0.05$, *** $p < 0.001$, n.s. not significant)
[1] *Picea abies*; [2] *Betula pubescens* / *Betula pendula*

and 12% for deadwood and uprooting related sites respectively. The microsite availability frequencies were more similar at the two northern-boreal areas than at Dvina-Pinega.

At all study areas the microsite occupancy frequencies of small seedlings ($h < 0.3$ m) and seedlings ($h \geq 0.3$ m, < 1.3 m) of spruce deviated from the availability frequencies (Fig. 2, Table 3). At Dvina-Pinega 80% of small spruce seedlings were on deadwood and only 10% on undisturbed ground. At Pallas-Ylläs and Kazkim the deadwood occupancy of small spruce seedlings was approx. 40%, whilst undisturbed ground occupancy was higher at approx. 40% at Pallas-Ylläs compared to only approx. 20% at Kazkim. At all study areas the undisturbed microsite occupancy for spruce seedlings increased slightly compared to small seedlings, but at Dvina-Pinega undisturbed ground occupancy for spruce seedlings remained lower than at the other areas, whilst 40% of seedlings were found on such microsites at Kazkim and Pallas-Ylläs. Deadwood microsites hosted >60%, approx. 40% and approx. 50% of spruce seedlings at Dvina-Pinega, Pallas-Ylläs and Kazkim respectively.

In contrast to the smaller strata the microsite occupancy pattern for spruce saplings ($h \geq 1.3$ m, DBH < 10 cm) at all study areas did not significantly deviate from the available microsite frequencies (Fig. 2, Table 3). At Dvina-Pinega 40% of spruce saplings were found on undisturbed ground, whilst in contrast to the other study areas, 40% grew on deadwood related microsites, although this was not a significant relationship. At Pallas-Ylläs and Kazkim the majority of spruce saplings grew on undisturbed microsites.

As with spruce, at all study areas the microsite occupancy frequencies of small seedlings ($h < 0.3$ m) and seedlings ($h \geq 0.3$ m, < 1.3 m) of birch deviated from the availability frequencies (Fig. 2, Table 3). At Dvina-Pinega, Pallas-Ylläs and Kazkim 40%, 50% and 80% of small birch seedlings respectively were found on uprooting related microsites, whereas only approximately 20% of seedlings were found on such microsites (Fig. 2). In contrast, deadwood related microsites were preferred over uprooting related microsites for small birch seedlings at Dvina-Pinega. Over 60% of birch seedlings at Pallas-Ylläs and Dvina-Pinega were found on deadwood related microsites, but the occupancy was closer to 30% at Kazkim where 50% of birch seedlings were growing on undisturbed ground.

The microsite occupancy pattern for birch saplings ($h \geq 1.3$ m, DBH < 10 cm) significantly deviated from the availability only at Dvina-Pinega and Pallas-Ylläs (Fig. 2, Table 3). While the occupancy frequency of deadwood related microsites for spruce saplings fell in comparison to seedlings at Dvina-Pinega, the deadwood occupancy for birch saplings remained approx. 60%. In comparison, at Pallas-Ylläs approx. 55% of birch saplings were found on undisturbed microsites and only 10% were found on deadwood, although the occupancy still significantly deviated from the availability due to approx. 30% of birch saplings growing on uprooting related microsites. Microsite occupancy of birch saplings at Kazkim did not deviate from the availability and >70% were found on undisturbed ground (Fig. 2, Table 3).

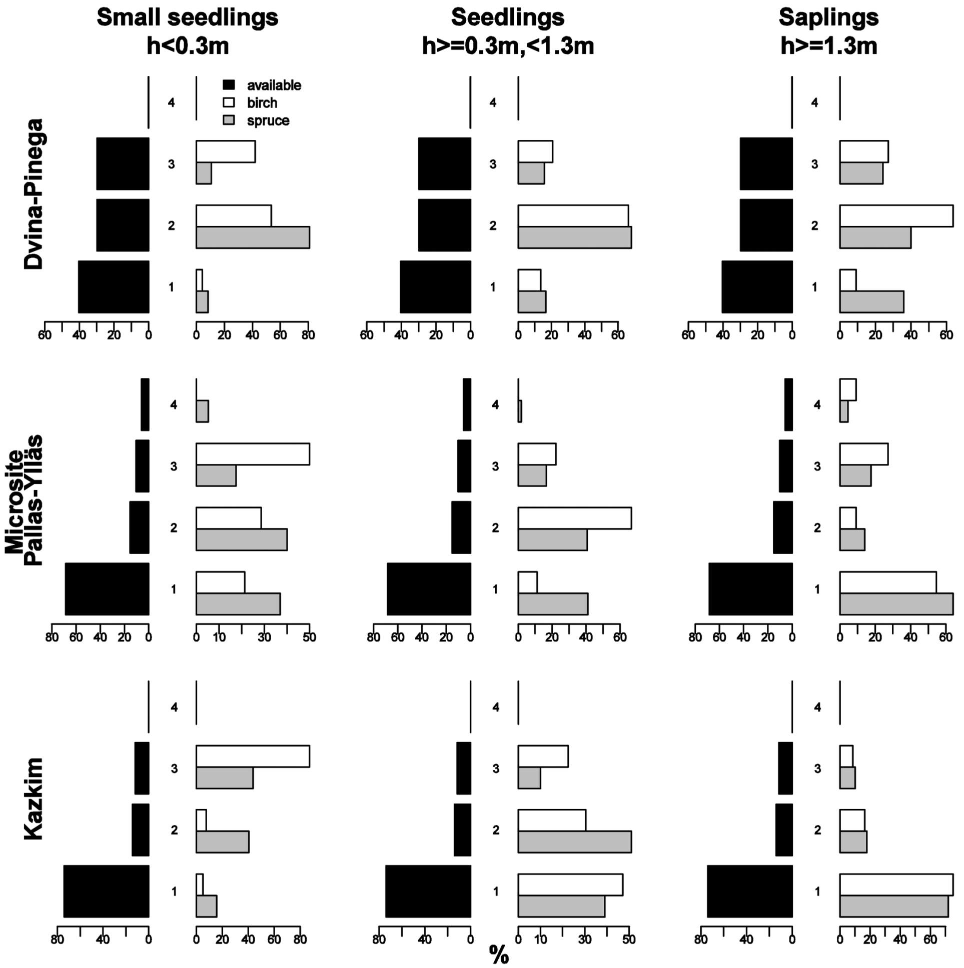

Fig. 2. Frequency of microsite availability (left) and microsite occupancy (right) for different regeneration size classes of spruce (*Picea abies*) and birch (*Betula pubescens* and *Betula pendula*). The microsites are: 1) undisturbed, 2) deadwood related (on or beside deadwood), 3) uprooting related (a root-plate mound or uprooting pit) or 4) other. Data from all stands was pooled by study area.

3.3 Spatial Correlation

Positive spatial correlation of both regeneration strata (for both spruce and birch) was exhibited in only 1 subplot at Dvina-Pinega, whilst Pallas-Ylläs displayed consistent positive spatial correlation at distances between 25 to 50 m, which was statistically significant in four of the five subplots (Fig. 3). At Kazkim positive spatial correlation of both regeneration strata (for both spruce and birch) was demonstrated in 3 subplots, but the spatial extent of the pattern (x-intercept) was more variable than at Pallas-Ylläs (Fig. 3).

Dvina-Pinega had marginal spatial correlation of spruce seedlings ($h < 1.3$ m) on only one subplot. Spruce seedlings exhibited significant spatial correlation on three subplots at Pallas-Ylläs, with two being marginally non-significant. Where significant, the spatial correlations were consistent in strength (approx. 0.5–0.6) and scale (approx. 40 m–50 m, Table 4). At Kazkim spruce saplings also exhibited significant spatial correlation on three subplots with a more variable spatial scale (approx. 40 m–75 m) and strength (approx. 0.5–0-7).

Spruce saplings ($h \geq 1.3$ m, $DBH < 10$ cm) at

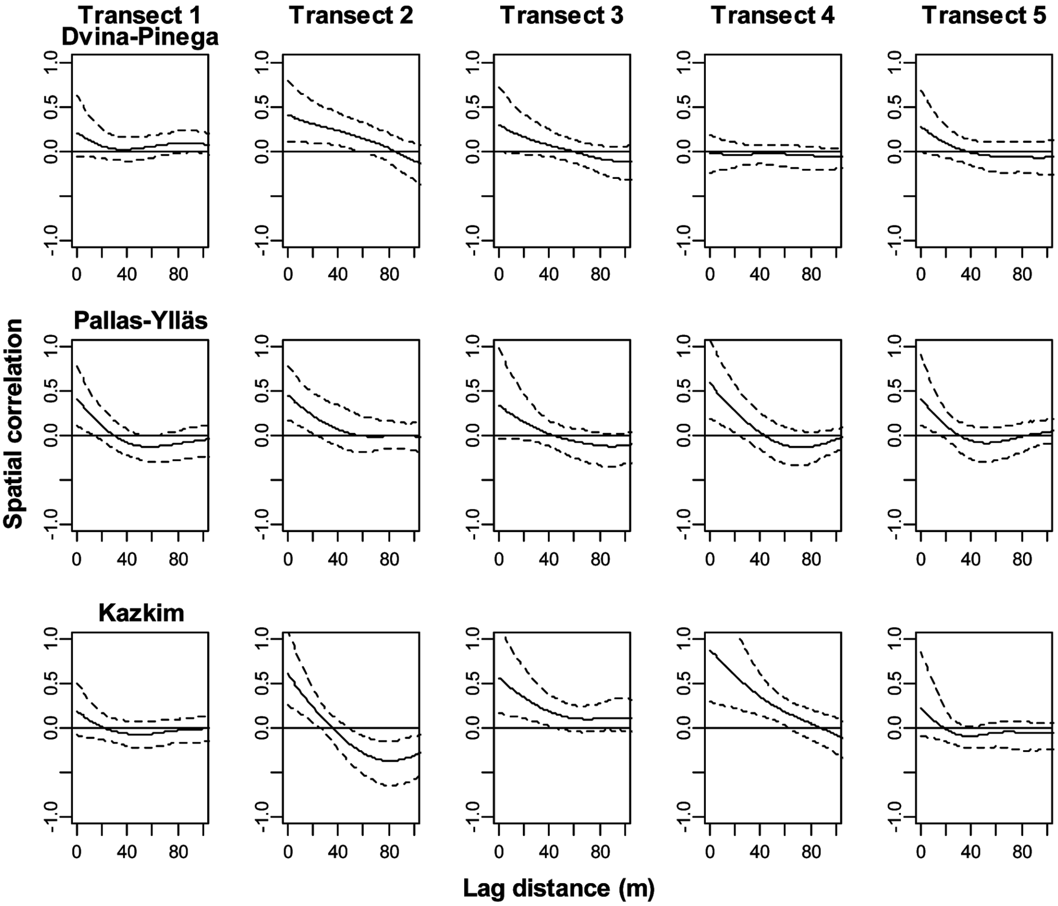

Fig. 3. Spatial spline correlograms for all regeneration (DBH < 10 cm) in the five plots in the three study areas. Dashed line indicates 95% confidence envelope.

Dvina-Pinega were significantly spatially correlated on three subplots, and the scale ranged between approx. 35 m and 40 m on two subplots while one had a scale closer to 55 m. Spruce saplings at Pallas-Ylläs also exhibited spatial autocorrelation of variable strength (approx. 0.4–0.7) but very consistent spatial scale (approx. 31 m–35 m) on four subplots. At Kazkim spruce saplings showed significant spatial correlation on three subplots with a fourth having marginal significance. These spatial correlations exhibited more variation in strength and the scale ranged from approx. 35 m–65 m.

Birch seedlings (h < 1.3 m) at Dvina-Pinega exhibited only some marginally significant spatial correlation on one subplot, and no significant spatial correlation was found at Pallas-Ylläs. Contrastingly, at Kazkim birch seedlings showed significant spatial correlation on three subplots and the other two were marginally non-significant. The strengths of the significant spatial correlations relationships at Kazkim ranged from approx. 0.4 to 0.65 and the scale was highly varied between subplots.

Birch saplings (h ≥ 1.3 m, DBH < 10 cm) at Dvina-Pinega were significantly spatially correlated on three of the four subplots (the fifth had no birch saplings). The relationship was very consistent on two of these subplots at approx. 35 m–40 m, while the third subplot had a spatial correlation scale of approx. 80 m. In contrast, at Pallas-Ylläs birch saplings exhibited no sig-

Table 4. Summary of spline correlogram analyses of regeneration by study area and plot.

Variable	Dvina-Pinega		Pallas-Ylläs		Kazkim	
Transect	x intercept	y intercept	x intercept	y intercept	x intercept	y intercept
a) SPRUCE SEEDLINGS [1]						
1	110.91	0.22	31.88	0.32	47.36	0.25
	(–60.18, 175.79)	(–0.07, 00.57)	(–118.56, 67.37)	(–0.08, 0.90)	(–134.74, 133.57)	(–0.13, 0.93)
2	90.15	0.40	41.84	0.57	20.83	0.25
	(45.95, 123.86)	(0.03, 0.91)	(20.73, 144.06)	(0.11, 1.24)	(–80.86, 163.81)	(–0.04, 1.10)
3	57.92	0.23	52.34	0.51	55.59	0.55
	(–68.33, 176.06)	(–0.09, 0.74)	(10.13, 190.14)	(0.02, 1.55)	(33.17, 189.92)	(0.13, 1.50)
4	–130.37	–0.02	48.75	0.65	74.17	0.74
	(–217.80, 152.20)	(–0.28, 0.20)	(29.05, 174.37)	(0.16, 1.86)	(58.88, 111.56)	(0.16, 1.96)
5	25.10	0.26	24.56	0.33	40.65	0.50
	(–98.66, 147.68)	(–0.11, 0.92)	(–61.66, 151.23)	(–0.02, 1.01)	(16.33, 77.40)	(0.08, 1.25)
b) BIRCH SEEDLINGS [2]						
1	122.10	0.28	17.05	0.20	29.96	0.34
	(–46.56, 357.69)	(–0.01, 1.74)	(–79.49, 45.78)	(–0.12, 0.58)	(–85.26, 130.23)	(–0.04, 1.35)
2	30.39	0.33	31.83	0.35	33.34	0.50
	(–36.19, 98.04)	(–0.01, 0.83)	(–75.00, 119.64)	(–0.01, 1.34)	(19.87, 58.01)	(0.09, 1.41)
3	25.60	0.17	26.21	0.23	129.67	0.43
	(–211.52, 140.30)	(–0.01, 0.76)	(–102.78, 177.25)	(–0.11, 0.65)	(39.67, 225.43)	(0.03, 1.12)
4	140.24	0.13	30.67	0.22	86.35	0.65
	(–102.17, 188.00)	(–0.22, 0.68)	(–215.28, 147.16)	(–0.14, 0.99)	(60.72, 128.56)	(0.16, 1.41)
5	26.70	0.29	62.34	0.34	39.47	0.33
	(–151.63, 58.23)	(0.10, 1.65)	(–13.53, 298.40)	(–0.04, 1.56)	(–54.91, 149.48)	(–0.02, 1.22)
c) SPRUCE SAPLINGS						
1	35.51	0.57	31.85	0.46	33.52	0.39
	(20.18, 77.32)	(0.06, 1.82)	(10.83, 70.15)	(0.06, 1.08)	(9.89, 152.31)	(0.03, 0.84)
2	27.20	0.30	34.96	0.67	50.15	0.36
	(–40.29, 139.27)	(–0.01, 0.83)	(25.42, 61.44)	(0.25, 1.23)	(–37.08, 75.21)	(–0.04.0.91)
3	24.54	0.33	127.41	0.19	64.05	0.27
	(–3.11, 65.08)	(–0.01, 0.82)	(–40.73, 186.08)	(–0.11, 0.55)	(31.35, 151.35)	(0.05, 0.50)
4	40.24	0.25	34.28	0.44	57.58	0.87
	(–90.64, 112.80)	(0.12, 0.64)	(16.42, 119.59)	(0.16, 0.82)	(43.62, 84.15)	(0.20, 2.29)
5	55.37	0.40	34.23	0.41	18.11	0.12
	(3.42, 78.24)	(0.01, 0.83)	(2.00, 53.28)	(0.01.1.19)	(–168.75, 87.30)	(–0.21, 0.52)
a) BIRCH SAPLINGS						
1	160.28	0.25	28.89	0.31	28.30	0.17
	(–41.91, 202.15)	(–0.01, 1.12)	(–59.01, 221.27)	(–0.02, 1.18)	(–134.66, 122.40)	(–0.21, 0.74)
2	36.24	0.51	55.50	0.32	39.53	0.61
	(16.44, 203.86)	(0.08, 1.42)	(–39.42, 97.46)	(–0.06, 1.00)	(26.68, 66.67)	(0.15, 1.23)
3	31.91	0.55	101.18	0.04	50.57	0.54
	(17.42, 198.06)	(0.10, 1.48)	(–128.43, 172.97)	(–0.29, 0.44)	(23.74, 163.79)	(0.12, 1.31)
4	80.90	0.58	28.93	0.18	107.62	0.55
	(38.20, 98.00)	(0.17, 1.44)	(–199.95, 155.09)	(–0.20, 0.86)	(18.44, 159.41)	(0.07.1.75)
5	–	–	29.76	0.27	27.01	0.29
	–	–	(–114.27, 242.55)	(–0.07, 1.22)	(–75.84, 129.09)	(–0.07, 1.24)

(values in parentheses are 95% upper and lower confidence limits)
[1] *Picea abies*; [2] *Betula pubescens / Betula pendula*

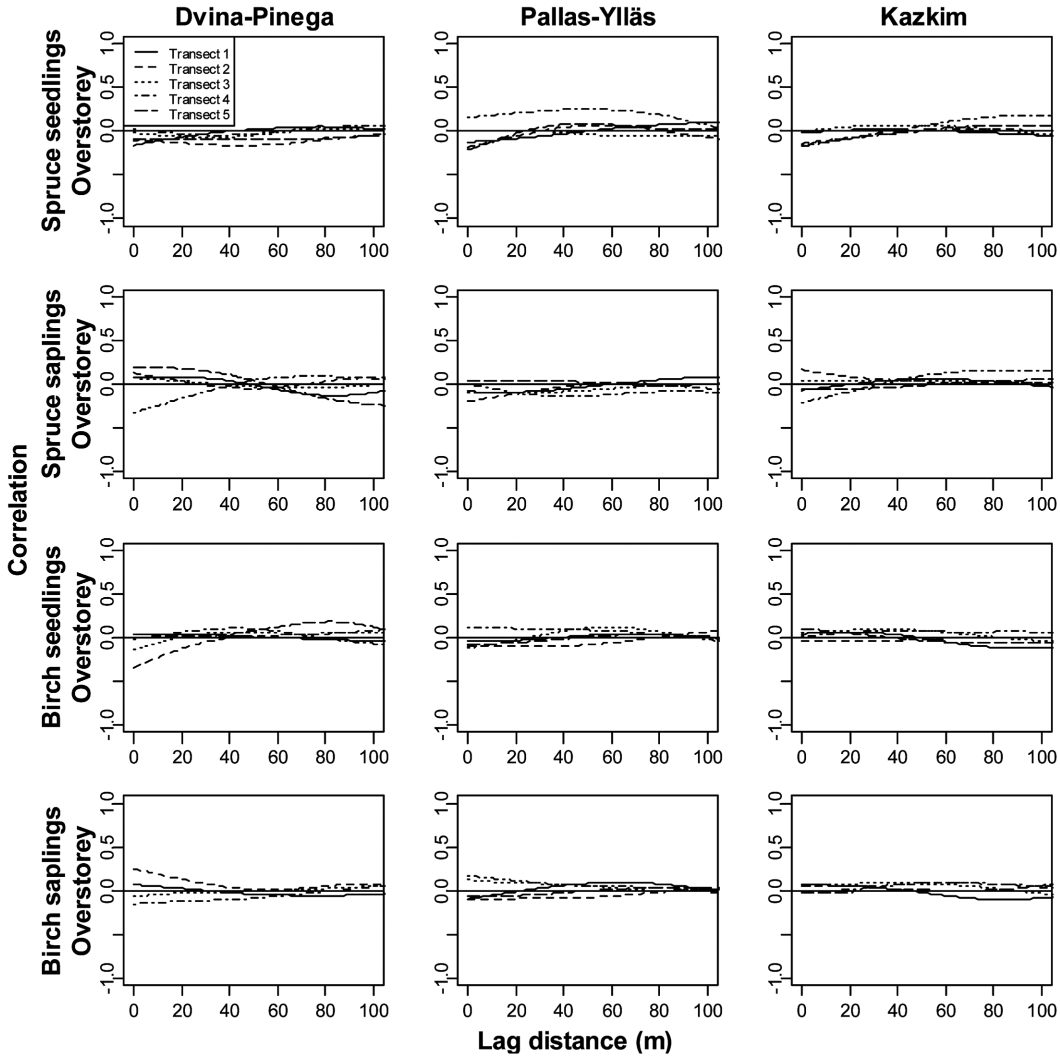

Fig. 4. Spline cross-correlograms of overstorey and regeneration components. All five plots are shown on a single plot, confidence envelopes are omitted to maintain clarity.

nificant spatial correlation, but three subplots were marginally non-significant. Birch saplings exhibited significant spatial correlation on the same subplots as the seedlings at Kazkim, and had consistent strength (approx. 0.6), though the spatial scale was variable.

No consistent patterns of spatial cross-correlation were found between seedlings or saplings of either spruce or birch and overstorey basal area (Fig. 4). Two subplots at Dvina-Pinega exhibited marginally significant weak segregation of birch seedlings and overstorey at a scale of ≤40 m. One subplot at Dvina-Pinega had marginally significant weak local segregation between spruce saplings and the overstorey. The other areas did not exhibit any significant local segregation or attraction between the strata for spruce or birch (Fig. 4).

4 Discussion

4.1 Forest Characteristics

The higher live tree density in the overstorey and regeneration strata at Dvina-Pinega compared to the two northernmost areas (Pallas-Ylläs and Kazkim) is congruous with the understanding that regeneration in the northern boreal forests is impeded by climatic and edaphic conditions which can limit seedbed availability (Sirén 1955; Lilja et al. 2006). Species composition is intimately linked to tree mortality. Species composition was thus broadly consistent with that theoretically expected to arise under each respective disturbance regime: the history of localised disturbance at Pallas-Ylläs and Dvina-Pinega (Aakala et al. 2009) has probably perpetuated spruce domination (Leemans 1991, Hofgaard 1993, Drobyshev 1999). The more recent mortality episode at Dvina-Pinega (Aakala et al. 2011) may have precipitated birch regeneration which could alter the species composition of the forest, although the ability of moderate-severity disturbance episodes to prompt a significant shift in tree species composition remains unclear (Fraver et al. 2008). In the Kazkim area the moderate-severity disturbance (Aakala et al. 2009) resulting from the simultaneous senescence of the relatively even-aged post-fire spruce cohort is likely to account for the recorded elevated share of birch in the regeneration strata. It is unclear if pulses of regeneration due to the senescence of the post-fire cohort at Kazkim will lead to another episode of synchronous senescence and regeneration (Shorohova et al. 2009) or if localized disturbance can expedite the transition to a shifting steady state mosaic (Bormann and Likens 1979).

4.2 Microsite Occurrence and Occupancy

The microsite availability frequencies at all study areas broadly concurred with previous studies (e.g. Hofgaard 1993, Kuuluvainen and Juntunen 1998, Ulanova 2000, Kuuluvainen and Kalmari 2003, Vodde et al. 2011). In the southern-boreal zone in Finland Kuuluvainen and Kalmari (2003) classified 28% of microsites as either on or beside dead wood in spruce forest, while Kuuluvainen and Juntunen (1998) classified 17% of their microsites as dead wood related in a pine forest. The uprooting microsite availability at all our study areas was also in accordance with the typical 7–25% coverage reported by Ulanova (2000). The frequencies of flat ground were slightly elevated compared to frequencies reported in similar studies, for example Kuuluvainen and Kalmari (2003) found 47% of microsites were flat ground at a disturbed Norway spruce dominated forest in southern Finland.

The importance of the microsites for regeneration was variable between species, area and strata, although small seedlings of both species preferentially occupied disturbed microsites at every area. Seedlings of both species also disproportionately occupied disturbed microsites, although at Dvina-Pinega undisturbed microsites were also important for the two smallest strata of spruce. Birch saplings, and to some extent spruce saplings, at Dvina-Pinega disproportionately occupied deadwood related microsites, although the relationship was not significant for spruce. This may be attributable in part to the greater frequency of disturbance microsites, but may also be due to exclusion of regeneration from the forest floor. It is generally understood that exclusion from the undisturbed forest floor occurs primarily due to competition with herbs and mosses (Maguire and Forman 1983, Harmon and Franklin 1989), canopy tree root competition and allelopathic attack (Korstian and Coile 1938) and lack of suitable seedbeds due to the moss-humus mat (Place 1955), resulting in a disproportionate number of seedlings on disturbance related microsites. The forest floor may be a more competitive environment at Dvina-Pinega due to the denser canopy, and, furthermore, the drought risk may be greater here than at the other areas (Aakala and Kuuluvainen 2011), which may cause the moss mat may rapidly dry out. It is understood that the non-sphagnum moss mats associated with drier environments make particularly poor seedbeds (Place 1955). Deadwood microsites may have less competition stress and better nutrient and moisture availability due to being in capillary contact with the mineral soil (Harmon and Franklin 1989, Gray and Spies 1997, Hörnberg et al. 1997, Zielonka and Niklasson 2001). The growth of mosses on deadwood has been suggested to have a beneficial impact on spruce regeneration (Hanssen 2003, Hunziker and Brang 2005), which may in part be due to mycorrhizal interaction (Eissenstat and Newman 1990). Nevertheless, it should be borne in mind that microsite occupancy can also be influenced by the proximity of seed sources, the timing and amount of seed production, as well as seed retention and predation (Harmon and Franklin 1989, Zielonka 2006, Vodde et al. 2011).

Somewhat paradoxically, spruce regeneration at every area had greater reliance on undisturbed microsites with increasing size, although this trend was less pronounced at Dvina-Pinega. Furthermore, at Pallas-Ylläs spruce regeneration in all strata showed some reliance on undisturbed ground. Spruce seedlings are understood to be subject to a particularly high mortality risk (Leemans 1991, Hofgaard 1993). This risk becomes particularly relevant in light of the reported low growth rates of spruce germinants on deadwood (Szewczyk and Szwagrzyk 1996, Kupferschmid and Bugmann 2005, Kathke and Bruelheide 2010). Growth rate can also be extremely retarded in the northernmost wet spruce forests in comparison to drier, more southerly forests (Sirén 1955). Seedlings on deadwood may have to persist for longer before recruitment, thus increasing the probability of mortality. Nurse logs may have intense inter-seedling competition (Kuuluvainen and Kalmari 2003), and once the moss layer becomes relatively thick, the competitive stress may be further increased due to the profuse growth bryophytes which could also heighten drought risk (Hörnberg et al. 1997, Zielonka and Niklasson 2001). The thickness of the moss layer and the species present will probably ultimately determine how moss affects spruce regeneration (Place 1955, Hörnberg et al. 1997). Fragmentation of the deadwood substrate can also affect long-term survival (Harmon and Franklin 1989). Disproportionately high regeneration on undisturbed mossy microsites may also occur due to browsing pressure (Kupferschmid and Bugmann 2005). Notwithstanding the above mortality risks, the trend of spruce saplings being found on undisturbed ground could also be due to the older disturbed microsites being classified as undisturbed. While this type of classification error is likely to account for some observations, the inclusion of regeneration growing beside dead wood in an advanced state of decay may have made the analysis more objective.

Birch seedlings and saplings at Kazkim also exhibited a disproportionate occupancy of undisturbed microsites, and at Pallas-Ylläs such microsites had an increased importance for birch saplings compared to the other two birch strata (seedlings and small seedlings). The low numbers of seedlings at Pallas-Ylläs require that caution is employed when interpreting the results. Nonetheless, uprootings can be particularly unstable leading to elevated mortality risk (Putz 1983), and litter and water accumulation in pits can kill all seedlings growing there. Browsing pressure can also be intensified on disturbed microsites as herbivores may preferentially target saplings which are elevated. Browsing damage is particularly pronounced for birch at Pallas-Ylläs (personal observation) where most regeneration was from birch stool sprouts which were not included in this analysis. At Kazkim overstorey senescence may have masked microsite importance for birch seedlings and saplings, as uprootings were indeed disproportionately occupied by small seedlings. As with deadwood, it should be borne in mind that many microsites which appear to be undisturbed may in fact be old disturbed microsites. Nevertheless, disturbed microsites may be less significant for survival and recruitment than establishment and for spruce at all areas and birch at the two northernmost areas.

4.3 Spatial Structure of Regeneration

The consistency of the pattern of spline correlograms of all regeneration at Pallas-Ylläs indicates that the regeneration had a clumped spatial pattern (Fig. 3).The Pallas-Ylläs plots have escaped significant allogenic disturbance for an extended time which should allow the forest to exist as a shifting steady state mosaic (Bormann and Likens 1979, Caron et al. 2009, Aakala et al. 2009). The relative consistency of the scale of the spatial correlation patterns for spruce seedlings and saplings across all five sub-plots at Pallas-Ylläs was therefore also expected (Table 4). It is immediately evident, however, that the spatial structure at the other areas of all regeneration is much more variable (Fig. 3). This indicates the regeneration process not analogous to that at Pallas-Ylläs, and that the forest may not exist as a fine-scale shifting mosaic.

In contrast to spruce, birch regeneration at Pallas-Ylläs showed no significant clumping at the scale of examination. One cause of this is that the regeneration strategy of birch is Pallas-Ylläs being highly reliant on sprouting. This regeneration strategy may be a response to the chronic pressure from reindeer and moose browsing (personal observation) that birch suffers. This disturbance agent was only significant at Pallas-Ylläs out of the all the study areas, and was constantly active over relatively large scales, obviously heavily retarding regeneration (personal observation).

There was less browsing from reindeer or moose at Kazkim, and the forest was also undergoing the senescence of a relatively even-aged spruce-dominated cohort which regenerated over 300 years ago (Aakala et al. 2009) which is likely to account for the precipitous birch regeneration. Shorohova et al. (2009) and Lilja et al. (2006) suggest that it may take several centuries after stand clearance for structure to stabilise. Both birch strata have a clumped pattern of variable spatial scale which would be expected given the patchy nature of senescence. The spruce strata at Kazkim also show a clumped pattern, which is congruous with the understanding that spruce advance regeneration can establish concurrently with birch (Drobyshev 1999). Nevertheless, despite the range of scales, the spatial correlation on some subplots was relatively local. This suggests that the forest developmental trajectory may tend toward a shifting fine-scale mosaic, although it remains to be seen if and when the forest spatial structure will attain this configuration.

Given the perceived defining role of moderate-severity disturbance from bark beetles and drought at Dvina-Pinega (Aakala et al. 2011), it may have been expected that these episodes would have created conditions conducive to birch regeneration exhibited through a larger scale of spatial correlation corresponding to larger disturbed patches (Drobyshev 1999, McCarthy 2001, Aakala and Kuuluvainen 2011). The larger scale of the spatial correlation for both birch strata on subplots one and four is indeed consistent with this concept, although the relationships were only significant in the sapling stratum (Table 4).

Regeneration at Dvina-Pinega takes place under a much denser canopy compared to the other study areas (Table 1). Although birch seedlings at Dvina-Pinega showed no consistent clumping, there was weak spatial segregation with the overstorey on one subplot. Likewise, no significant clumped pattern was found in the spruce seedling stratum, and spatial segregation with the overstorey was only detected on one subplot for the sapling stratum. If gap and patch disturbance-related changes are indeed the main drivers of regeneration then consistent spatial segregation of the strata could perhaps be expected. However, no consistent segregation between the overstorey and understorey was found. Similar findings have been made in other studies (e.g. Lundqvist and Fridman 1996, Manabe et al. 2000, Saksa and Valkonen 2011). One explanation for this apparently paradoxical finding is that high mortality from self-thinning and competition with the overstorey may have produced a less-clumped spatial pattern (Ford 1975, Chen and Bradshaw 1999), thus spruce saplings were significantly clumped on the three plots where no local segregation was recorded.

The ‘regeneration gap’ concept, as related to increases in light after gap disturbance, has its origins in studies on the dynamics of temperate forests (Watt 1947, McCarthy 2001). However, the northern boreal forest is fundamentally different to temperate forest in that the overstorey is naturally sparse due to slow growth and nutrient deficiency. It is perhaps significant that the only local segregation between the regeneration and overstorey strata was found at Dvina-Pinega where the canopy is less sparse. At northern latitudes the light changes caused by gap formation may be expressed outside the physical gap due to oblique sun angles (Ban et al. 1998, Kuuluvainen et al. 1998) which could also affect spatial relationships. At all study areas a significant limiting factor may be below ground competition, especially for nitrogen, rather than light (Kuuluvainen 1994, McCarthy 2001). The changes in root competition within gaps are poorly understood and may be highly variable spatially (Kuuluvainen 1994). The spatial structure of the overstorey may not therefore correspond to actual resource heterogeneity affecting the regeneration (Bazzaz and Wayne 1994). Resource heterogeneity within gaps is also affected by microsite diversity, and the interaction of overstorey gaps and microsites may also influence spatial cross-correlation of overstorey basal area and regeneration. Also, heterogeneity within the patch or gap, in part arising from microsite influence, would suggest that the areas of overstorey discontinuity are not evenly colonised by regenerating trees (Gray and Spies 1997).

Other factors may ultimately be responsible for the clumping patterns detected. The influence of seed production is often overlooked as significant control on the spatial pattern of regeneration (Houle 1992). The abundance of seed producing adults can be very variable, which could have a pronounced influence on regeneration. The timing of seeding, and the copiousness, fecundity and predation of the seed are also important variables with a strict temporal reliance due to the seed bank being of limited influence in the boreal zone (Hokkanen 2000). The preference for disturbed microsites may also be responsible for much of the clumping where they are preferentially occupied (Manabe et al. 2000).

4.4 Variation in Regeneration Dynamics

The results provide further evidence for the notion that regeneration in primeval spruce forests is subject to a highly complex set of interdependent factors, all of which demonstrate great temporal and spatial variability. Disturbance microsites appear to be important for seedling establishment at all areas, but other factors may have increased significance for long-term regeneration survival, especially for spruce. This may arise from increased competition pressure, drought risk due to profuse bryophyte growth and browsing damage on disturbed microsites (Hörnberg et al. 1997, Zielonka and Niklasson 2001, Kuuluvainen and Kalmari 2003, Kupferschmid and Bugmann 2005). At Dvina-Pinega all strata relied on disturbed microsites, particularly deadwood related, where the most fundamental differences with the other areas is the degree of overstorey closure, increased drought risk and lack of browsing pressure, which together may account for this difference. Furthermore, the only spatial segregation found between the overstorey and regeneration was at Dvina-Pinega. However, spatial segregation coincided with generally weak regeneration clumping, which suggests that the dense overstorey influence may result in a less strong clumped pattern (Ford 1975, Chen and Bradshaw 1999). The stronger clumping at the other study areas and strata may result from local competition between seedlings and other floral constituents becoming more important where the overstorey influence is less significant, although the influence of seed production, dispersal and predation should not be underestimated (Houle 1992, Hokkanen 2000). The regeneration-gap concept may therefore not be a useful model for regeneration in northern boreal spruce forests, however, the possibility of below ground interaction and diffuse light may account for the lack of spatial segregation.

In the Dvina-Pinega area the high share of spruce in the overstorey and the findings from this study (little birch regeneration) suggest that past gap dynamics (Aakala et al. 2011) have favoured spruce. However, the recent larger disturbance, which ended in 2004, killed a considerable proportion of trees (on average, 21%). This may have created conditions more suitable for birch recruitment. At Pallas-Ylläs birch was highly dependent on sprouting and had extensive pressure from browsing. Despite the apparent continuity of the disturbance regime shown by the spatial structure of spruce in both strata, this has not allowed sexual birch regeneration. Based on what is known of the current disturbance regime (Caron et al. 2009, Aakala et al. 2009), the influence of reindeer and moose probably favours spruce recruitment in Pallas-Ylläs, with birch possibly being able to survive in stools. The larger scale disturbances and variable spatial structure at the other areas raises questions of stability and of the spatiotemporal typicality of such events regionally. At Kazkim the conditions ushering the profuse birch regeneration currently recorded would be expected to lead to birch comprising a larger compositional share.

4.5 Conclusions and Management Implications

This study confirms the importance of disturbance related microsites for regeneration establishment and early growth, but demonstrates that long-term survival may be more probable elsewhere. Furthermore, the regeneration gap concept does not appear to be useful for northern boreal spruce forests due to the lack of consistent, strong spatial segregation between the understorey and overstorey. Fundamentally, our results show considerable differences and variation exists in the natural regeneration pattern amongst the study areas. Assessing the typicality of the findings is necessary to better understand the full extent of the range of variability in the studied processes across the region to provide a baseline for forest management and conservation initiatives inspired by natural forests.

We employed a consistent methodology to document the regeneration processes and characteristics in question at three study areas which, by definition, lie within the natural range of variability (NRV). A comparative study employing consistent methods on five 1.6 ha plots at three separate study areas is quite unprecedented, and, as such, provides a invaluable means of investigating and comparing the NRV of the studied phenomena. This will therefore enhance understanding of regeneration processes in forests where natural stand-replacement is a rare event, thus also informing benchmarking for natural disturbance emulation and restoration initiatives.

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